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Arthropod communities in a maritime Antarctic moss-turf habitat: Life history strategies of the prostigmatid mites

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With 7 figures

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Contents

1. Introduction

The Prostigmata have received much less attention from soil zoologists than Acari in the orders Cryptostigmata and Mesostigmata. The small size of the Prostigmata, as well as the difficulties of identification, largely account for this neglect. However, Luxton (1981) tabulated twenty-five studies on soil Prostigmata populations, and Petersen & Luxton (1982) reviewed the estimates of mean population density in the Prostigmata from eighty-four sites. These showed a wide range of densities up to 2×10^5 m^{-2}. The Prostigmata are the most abundant mites in moss-turf habitats in the maritime Antarctic (Tilbrook 1967; Goddard 1979; Usher & Booth 1984).

Moss-turf habitats on Signy Island, South Orkney Islands, are composed of two dominant turf-forming mosses, *Chorisodontium aciphyllum* (Hook. f. & Wils.) Broth. and *Polytrichum alpestre* Hoppe, with a low density of both fructicose and encrusting lichens and leafy liverworts. A semi-ombrogenous peat of pH 4.5—5.0 accumulates, which, in the maritime Antarctic, can become incorporated into a permafrost layer (Fenton & Lewis Smith 1982). A species-poor arthropod community, largely composed of two species of Collembola, one species of predatory Mesostigmata and three genera of Prostigmata, occurs in this habitat. Other species of mites and Collembola are also present in small numbers, especially in peripheral areas (Goddard 1980; Usher & Booth 1984).

Goddard (1979), working with sets of randomly located cores collected monthly, studied the population dynamics of the four mite taxa over a period of twenty-seven months. For the three prostigmatid mites, he divided the populations into three developmental stages — larvae, nymphs and adults. During studies on the spatial distribution of the arthropods in the same moss-turf site, Booth & Usher (1984), and Usher & Booth (1984, 1986) recorded the numbers of mites in each developmental stage, i.e. larva, protonymph, deutonymph tritonymph (this stage is not present in the Mesostigmata) and adult. The aim of this paper is to summarize the data on the developmental stages of the prostigmatid mite taxa so as to deduce features of their life histories.

2. Methods

Samples were collected from the Signy Island terrestrial reference site 1 (60°44′ S, 45°35′ W) during the two austral summers of 1980/81 and 1981/82, except for those collected on 20 January 1982 from a moss-turf near the British Antarctic Survey's Signy Island station at Factory Cove. SIRS 1, described by TILBROOK (1973), is a moderately sloping, extensive moss-turf interspersed by a few large boulders and wetter runnels. It has been subject to a number of ecological and energetics studies, summarized by DAVIS (1981). The samples for the present study were collected from well developed moss-turf, and all cores were cut to 9 cm deep. The cores were either 5 cm square and contiguous (from grids or transects) or were circular, 6 cm in diameter, and randomly distributed.

Arthropods were extracted by high gradient extraction, as described by USHER & BOOTH (1984), from samples either 1.5 or 3.0 cm thick. The mites were counted, identified, and assigned to a developmental stage after clearing them in 30 percent lactic acid in a cavity slide and observing them under phase contrast microscopy at a magnification of ×400. The data for each sampling occasion have been converted to density estimates (numbers per m²) or to proportions of a taxon in a particular developmental stage so that the counts from different kinds of samples can be compared. The density estimates are not intended to be population estimates due to the contiguous nature of many of the samples (as discussed by USHER & BOOTH 1984). Even if soil cores had been taken randomly, they still would not have taken a random sample of the mites in the moss-turf, and hence confidence intervals are only tentatively used for the estimates of proportions quoted here. The observed densities of arthropods vary greatly on different sampling occasions, and it is possible that the extraction efficiency of the younger developmental stages is less than that of the older stages. However, in order to interpret the proportional data, it is necessary to assume that the relative extraction efficiencies of each developmental stage of a taxon, compared with the extraction efficiencies of the other developmental stages of the same taxon, remain constant throughout the season. There are no data either to validate or to invalidate this assumption, which is also inherent, though rarely stated, in virtually all ecological studies of soil microarthropods. One indication that the assumption may not always be valid is that HALE (1980) estimated that less than 30 percent of the first instar individuals of *Onychiurus procampatus* were extracted compared with the older instars.

3. The taxa

Three genera of prostigmatid mites were present in sufficient abundance for study. *Nanorchestes berryi* STRANDTMANN was the only species of *Nanorchestes* present in the moss-turf. Although this species has only recently been described (STRANDTMANN 1982), its developmental stages could be identified by reference to LINDSAY (1972). The developmental stages of *Ereynetes macquariensis* FAIN have recently been described by BOOTH (1983). Three species of the genus *Eupodes* were found in the samples, and these are described by BOOTH, EDWARDS & USHER (1985). The predominant species, *Eupodes parvus* BOOTH *et al.*, accounted for about 95 percent of specimens from SIRS 1, *E. exiguus* BOOTH *et al.* for about 5 percent, and only a single specimen of *E. minutus* (STRANDTMANN) was collected. Separation of the species has not been attempted in these samples, and hence counts were combined as *Eupodes* spp. (BOOTH & USHER 1984; USHER & BOOTH 1984). GODDARD (1980) described the developmental stages of *Eupodes* from SIRS 1 under the name *E. minutus*.

In addition, four other species were encountered in small numbers. *Pretriophtydeus tilbrooki* (STRANDTMANN) was occasionally found together with its variant forms, referred to by STRANDTMANN (1967), which are now believed to represent a distinct species in the genus *Apotriophtydeus* (ANDRÉ 1980). *Stereotydeus villosus* (TROUESSART), which occurred infrequently, is abundant in other habitats, such as under both stones and small cushions of moss, whilst *Halotydeus signiensis* STRANDTMANN & TILBROOK is less abundant and usually restricted to damper habitats than the moss-turf.

For simplicity, taxa will be referred to by their generic names throughout the text. Mites in family Tydeidae are referred to collectively as *Tydeus* spp.

4. Results

4.0. General

The counts of Prostigmata, extracted from moss-turf samples collected on eight occasions during the 1980/81 summer and on seven occasions during the 1981/82 summer season, are shown in Table 1.

4.1. *Ereynetes*

Ereynetes showed a well defined succession of developmental stages throughout both seasons (Fig. 1). During the first season, larvae occurred almost exclusively in December and January, with a peak in the second half of December. In the second season, larvae persisted later into the summer (Fig. 2). Protonymphs peaked around the middle of January,

Table 1. Total counts of prostigmatid mites extracted from moss-turf samples from Signy Island, South Orkney Islands

Taxa	Sampling date							
	10 XII 80	19 XII 80	25 XII 80	10 I 81	23 I 81	4 II 81	15 II 81	20 II 81
Nanorchestes berryi STRANDTMANN	25	37	177	194	317	370	133	62
Ereynetes macquariensis FAIN	9	51	182	165	274	317	203	122
Eupodes spp.	50	69	792	820	233	1,124	748	270
Tydeus spp.	0	0	1	2	4	0	0	0
Stereotydeus villosus (TROUESSART)	0	0	1	0	0	4	0	0
Halotydeus signiensis STRANDTMANN & TILBROOK	0	0	0	0	0	0	0	0
	Sampling date							1980—1982
	9 XII 81	16 XII 81	29 XII 81	9 I 82	20 I 82	8 II 82	30 III 82	Total
Nanorchestes berryi STRANDTMANN	15	550	533	490	391	693	148	4,135
Ereynetes macqariensis FAIN	6	212	1,078	982	472	576	38	4,687
Eupodes spp.	116	1,440	2,608	2,222	5,037	2,124	1,025	18,678
Tydeus spp.	1	38	3	0	5	8	0	62
Stereotydeus villosus (TROUESSART)	0	0	0	0	26	13	2	46
Halotydeus signiensis STRANDTMANN & TILBROOK	0	3	0	0	0	1	0	4
Overall **total**								**27,612**

Note: Samples of various sizes were collected on fifteen occasions from December 1980 until March 1982 inclusive.

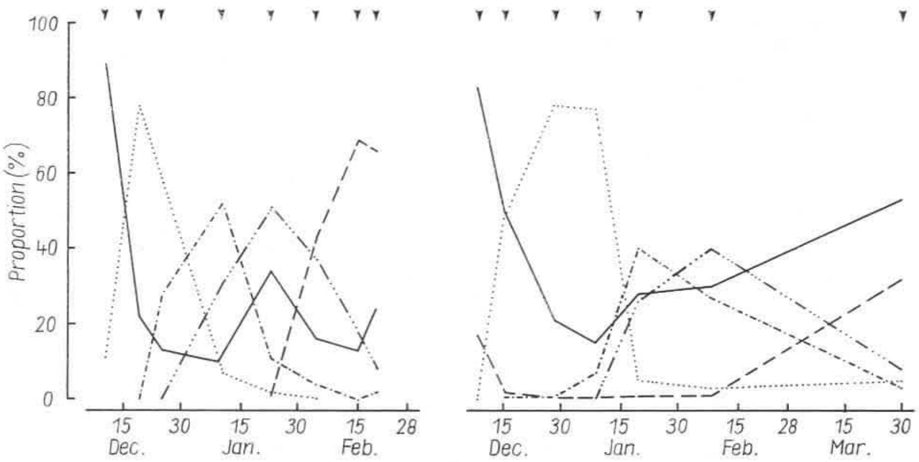

Fig. 1. The proportions of the developmental stages of *Ereynetes* in eight sets of samples during the 1980/81 austral summer (at left) and in seven sets of samples during the 1981/82 summer (at right). The sampling dates are indicated by the arrow heads. The instars are represented by the following lines: ········ larvae, ·—·—· protonymphs, —···— deutonymphs, — — — tritonymphs, ——— adults.

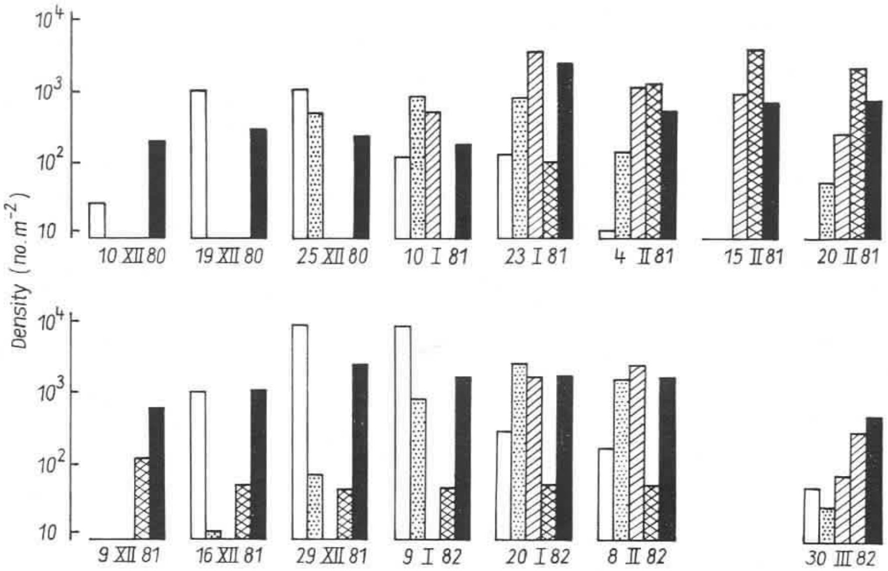

Fig. 2. The density of *Ereynetes* in samples collected from Antarctic moss-turves on Signy Island between December 1980 and March 1982. Open bars (□) indicate the number of larvae, and black bars (■) the number of adults. Protonymphs (▦), deutonymphs (▨) and tritonymphs (▩) are indicated by increased density of shading of the bars, the developmental stages running from left to right of each diagram. Absence of a bar implies absence of that developmental stage from the sample.

followed by deutonymphs in late January and February. No tritonymphs were sampled until the second half of January in the first season, although small numbers were present throughout the second season. Logistic arrangements precluded sampling in late summer (March), when a peak of tritonymphs would be expected. Such a peak would be followed by an increase in the proportions of adults. The presence of teneral adults in the early December and in the 30 March 1982 samples suggested that a proportion of tritonymphs moulted in late autumn, whereas others overwintered and moulted into adults in the following spring.

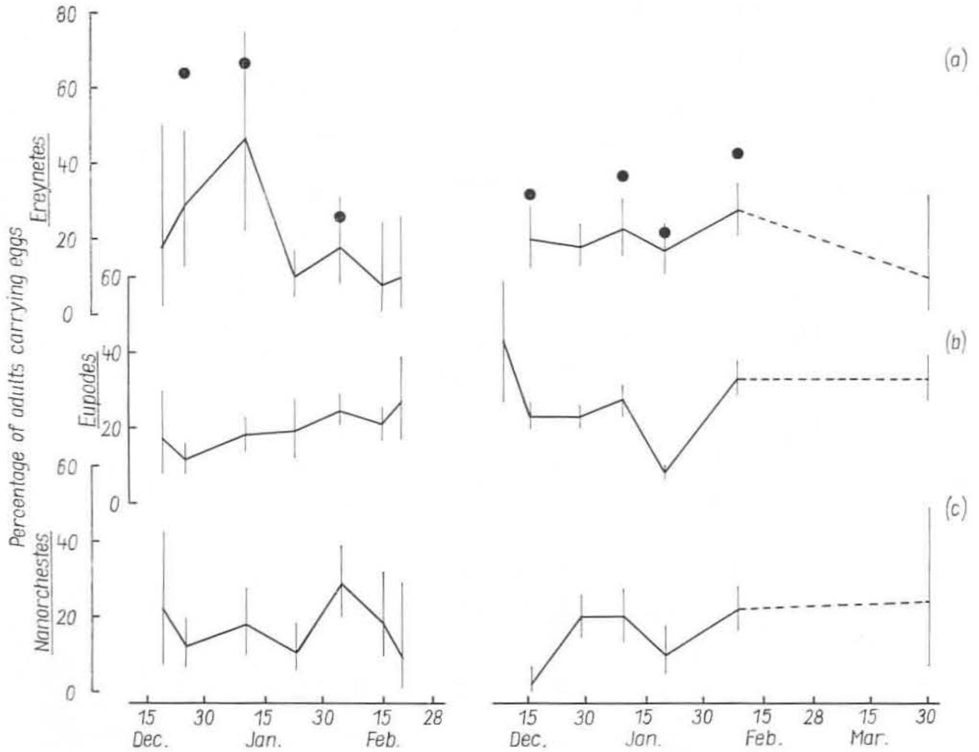

Fig. 3. The proportions of the adult mites of the three commonest taxa carrying eggs, based on data from 15 samples between December 1980 and March 1982. The vertical bars indicate approximately 95 percent confidence intervals for the estimated mean percentage. Usually the adults were not sexed, and hence the proportions relate to the total adult population. For seven sets of samples, *Ereynetes* was sexed, and the black dots indicate (without confidence limits) the proportions of females carrying eggs. The graphs to the left are for the 1980/81 austral summer, those to right for the 1981/82 summer.

Adult female *Ereynetes* were fecund throughout the summer, during which time they were never observed to be carrying more than a single egg inside their bodies. In seven of the fifteen sets of samples, the adults were sexed, and females were significantly more abundant than males ($\chi^2 = 76.4$, 7 d.f., $P < 0.001$), outnumbering males by approximately 2 to 1. Fig. 3a shows the percentage of the adult population carrying eggs, and the additional dots represent the proportions of adult females with eggs. Although there is a peak of egg carrying activity in the first half of January in the first season, in the second season the proportion of egg carrying adults remained reasonably constant.

4.2. *Eupodes*

Apart from the first sampling occasion (10 December 1980) when larvae and protonymphs were absent, all developmental stages of *Eupodes* were present in all samples (Fig. 4). Compared with the data for *Ereynetes*, the peaks of occurrence of the developmental stages were much less pronounced. However, in both seasons, the proportion of larvae peaked during January, and protonymphs peaked about four weeks later (Fig. 5).

The proportion of adults bearing eggs varied between about 10 and 30 percent in the first season, although this proportion increased slightly during the season (Fig. 3b). At the beginning of the second season, a larger proportion of the adults bore eggs (although the sample size was relatively small), whilst the 20 January 1982 sample had a much reduced

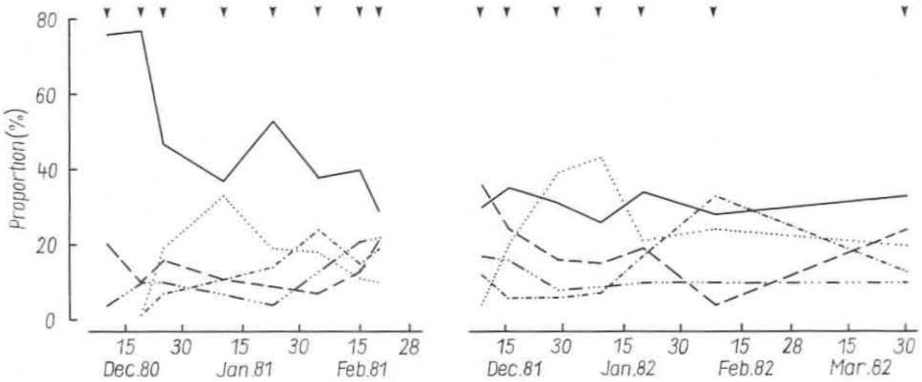

Fig. 4. The proportions of the developmental stages of *Eupodes* in 15 samples collected between December 1980 and March 1982. The symbols and lines used are as in Fig. 1.

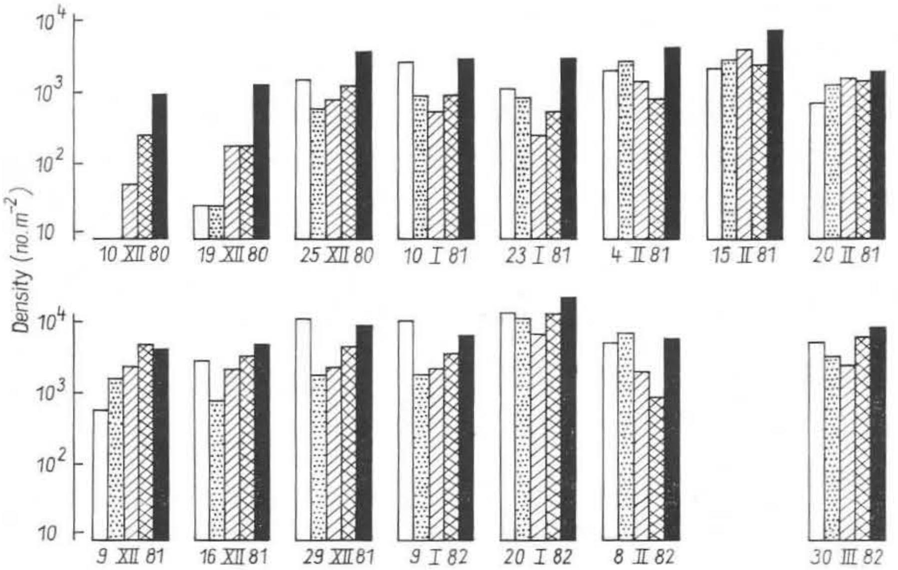

Fig. 5. The density of *Eupodes* in 15 samples collected between December 1980 and March 1982. The shading of the bars is as in Fig. 2.

proportion of egg bearers. This latter sample was taken from the Factory Cove moss-turf site, where *E. parvus* and *E. exiguus* were present in approximately equal numbers, and hence it is possible that the two species have different life-history strategies. Overall, the majority of egg-bearing individuals (1,075) had a single egg, but 146 (11.8 percent) carried two eggs, and 14 individuals (1.1 percent) bore three eggs at the same time.

4.3. *Nanorchestes*

All developmental stages were present throughout the two summer seasons, except for protonymphs which were absent from the 19 December 1981 sample (Fig. 6). During both summers, larvae showed peaks of occurrence in December, and in the first season, there appeared to be a small secondary peak of larvae in early February. The proportion of protonymphs peaked in January, although the numbers of individuals remained reasonably large

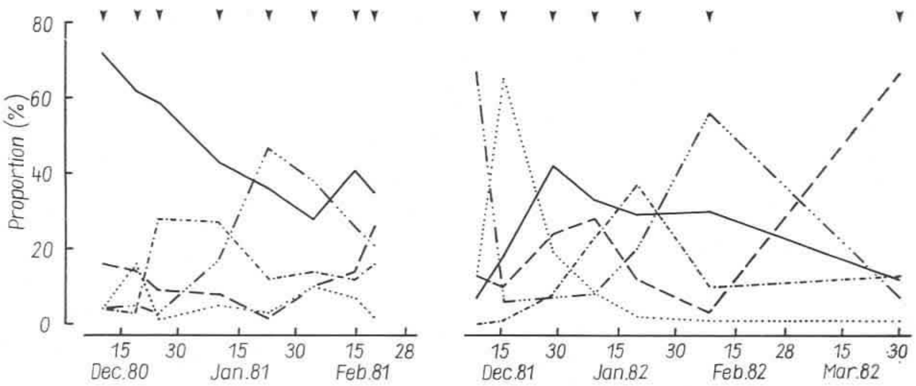

Fig. 6. The proportions of the developmental stages of *Nanorchestes* in 15 samples collected between December 1980 and March 1982. The symbols and lines used are as in Fig. 1.

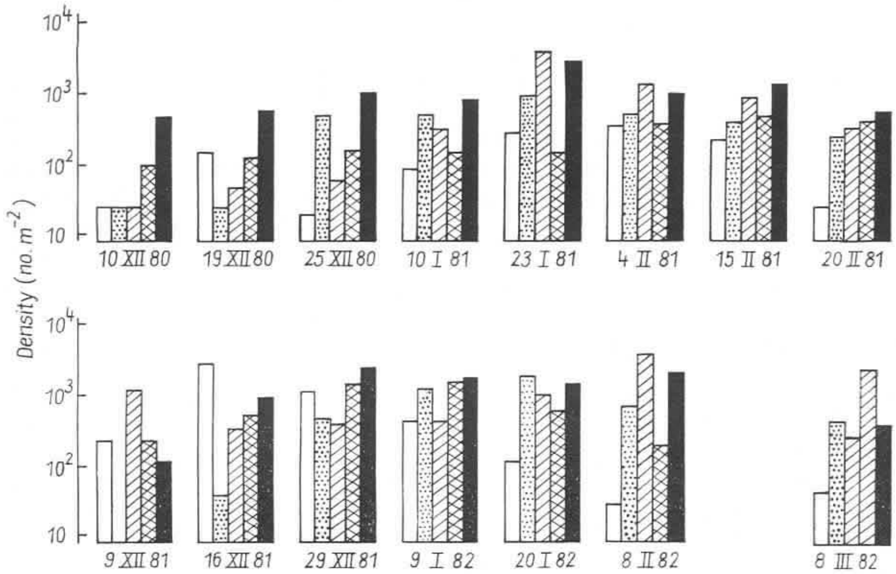

Fig. 7. The density of *Nanorchestes* in 15 samples collected between December 1980 and March 1982. The shading of the bars is as in Fig. 2.

during the rest of the season. In the first season, the proportion of deutonymphs peaked in late January. In the second season, there was a very large proportion of deutonymphs in the first December sample, which declined rapidly, and was then followed by another peak in early February (Fig. 7). The numbers of tritonymphs showed an increasing trend in the second half of the first season, but an early January peak in the second season, and they were dominant at the end of March 1982.

In the eight samples where the adults were sexed, the sex ratio was not significantly different from 1 : 1 ($\chi^2 = 4.83$, 8 d.f., $0.95 > P > 0.05$). Fig. 3c shows the proportion of adults bearing eggs during the two seasons. Although the proportions in the first season appear to follow a similar trend to the proportion of larvae in the samples, there appears to be little significant variation: only the increase from 23 January to 4 February 1981 would appear to be significant. Similarly, in the second season, there is no evidence for any variation

in the proportion of egg bearers except for the reduced proportion in the 16 December 1981 sample. Overall, the majority of fecund females carried a single egg, but 8 out of 226 (3.5 percent) carried two eggs.

5. Discussion

In order to propose life-history strategies for the three taxa of prostigmatid mites in the moss-turf, it is necessary to extrapolate the results from two summer seasons only, and to make use of the information in previously published work. *Ereynetes* shows the most clear cut behaviour of the three taxa. The predominance of larvae in the second half of December and the first half of January followed by the peaks of occurrence of the nymphal stages shows that development from egg-hatching to tritonymph takes place during a single summer season. The presence of teneral adults in the March and early December samples suggests that a certain proportion of the tritonymphs moult to adults at the end of the first summer, whilst the rest overwinter and moult to adults in spring. Adult females were observed carrying eggs throughout the summer. Given the data on larval abundance, it is likely that the vast majority of these eggs do not hatch in the summer in which they were produced, but overwinter and hatch no earlier than in the following spring, although it is possible that a few eggs laid early in the spring may hatch in the same summer. If eggs were hatching as they were laid, one would not expect such a large early summer peak of larvae. Although development of *Ereynetes* from egg hatching to adult may be completed within a single year, the eggs also spend at least almost a year in the moss-turf and thus the generation time for most individuals is likely to be two years.

GODDARD (1979) showed that both adults and nymphs overwintered. However, he was not able to distinguish the nymphal stages, and by sampling only once a month during the summer, he was not able to resolve the peaks of occurrence of the juvenile stages which were observed during the present study. He also occasionally found larvae during the winter, and the presence of larvae in the autumn was confirmed by the few individuals that were found in the March 1982 samples (see Fig. 2). As GODDARD suggested, it is quite likely that these autumn and winter larvae hatched out from eggs in the cores as they were being extracted when the rapid rise to well above freezing temperatures would be conducive to egg hatching. It is, therefore, probable that larvae do not overwinter in the field.

One question remains unanswered; for how long do the adults live? Adults are able to overwinter and there is therefore the possibility that they could have more than one reproductive season. Such a strategy, if it exists, would enable the population to persist at a low level in the event of a very poor summer when juvenile survival was low. In addition, having more than one overwintering strategy (i.e. eggs and either tritonymphs or adults) may be an adaptation to coping with different environmental stresses during the winters, which are known to vary in their intensity from year to year.

Eupodes shows a much less clear cut pattern than *Ereynetes*. Although there is a broad peak in the proportion of larvae in January, large numbers of larvae continue to exist throughout the season, suggesting that eggs hatch soon after they are laid by the females. The proportion of protonymphs peaked about four weeks after the larval peak, but no other obvious peaks of occurrence were detected by the sampling regime. It seems probable that, with the possible exception of the larvae, all stages overwinter, and that development from larvae to adult cannot be fitted easily into a single summer season. Thus there is no penalty involved if larvae appear late in the summer, and breeding is therefore almost continuous as long as climatic conditions allow. It is suggested that the mean generation time is two to three seasons, allowing for the time from egg laying to egg hatching, as well as time for the development through to the adult female becoming fecund.

Nanorchestes, likewise, shows a less clear cut pattern than *Ereynetes*, although the proportions of the developmental stages in the second season do show successive peaks. Although there was a definite peak of larvae in the second season in December, they were present in larger numbers throughout the first season. With the probable exception of the larvae, all developmental stages would appear to overwinter. It is suggested that *Nanorchestes* has a

similar developmental strategy to *Eupodes*, although it would appear from the weak succession of peaks in the second season that *Nanorchestes* is able to develop faster than *Eupodes*. A mean generation time of two years is therefore suggested.

West (1982) studied the life histories of three species of mites on the sub-Antarctic island of South Georgia, and he concluded that mites from temperate zones "typically show an annual cycle, so that each stage, excluding the adult, is present for only a short period during the year. On South Georgia, the seasons are not predictable enough for this to be a viable strategy". He considered that the South Georgian mites demonstrated two strategies: long lived adults with reproduction in several seasons and, alternatively, adults that produce a large pulse of offspring and then die. There is no evidence for the latter strategy in the Antarctic Prostigmata, though, with the presence of some larvae and protonymphs throughout much of the austral summer, some evidence for the former strategy. This was also demonstrated for *Gamasellus racovitzai* (Mesostigmata) on Signy Island by Lister (1984). Breeding of these mites has a seasonal element, but there is evidence of nymphal stages throughout much of the Antarctic summer when soil temperatures can be expected to be above zero and the mites active. The other feature of *G. racovitzai* is that the generation time is protracted; Lister (1984) suggested a generation time of about 3 years. The studies of *Ereynetes*, *Eupodes* and *Nanorchestes* in Figs. 1, 4 and 6 indicate generation times of 2 or more years. Although the life histories of the Collembola and Cryptostigmata have yet to be investigated in detail, it appears that these Antarctic soil arthropods have adopted reasonably flexible life history strategies, and that the generation times are well in excess of one year. Based on an analysis of morphometric data from laboratory reared individuals Burn (1981) estimated that the largest field specimens of *Cryptopygus* from the Antarctic may be at least 3 to 7 years old. Although it is difficult to prove which factors have influenced the development of any particular life history strategy, West (1982) argued convincingly that it was the unpredictability of these polar environments that had led to strategies that are sufficiently flexible for the spedies to survive a number of extremely different seasons.

6. Acknowledgements

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7. References

André, H. M., 1980. A generic revision of the family Tydeidae (Acari: Actinedida). VI. Generic descriptions, keys and conclusions. Bull. Ann. Soc. belge. Ent. **116**, 103—130, 139—168.

Booth, R. G., 1983. A description of the juvenile life-stages of the Antarctic mite *Ereynetes macquariensis*. British Antarctic Survey Bulletin 61, 7—12.

— & M. B. Usher, 1984. Arthropod communities in a maritime Antarctic moss-turf habitat: effects of the physical and chemical environment. J. Anim. Ecol. **53**, 879—893.

— M. Edwards & M. B. Usher, 1985. Mites of the genus *Eupodes* (Acari, Prostigmata) from maritime Antarctica: a biometrical and taxonomic study. J. Zool., London, **207**, 381—406.

Burn, A. J., 1981. Feeding and growth in the Antarctic collembolan *Cryptopygus antarcticus*. Oikos **36**, 59—64.

Davis, R. C., 1981. Structure and function of two Antarctic terrestrial moss communities. Ecological Monographs **51**, 125—143.

Fenton, J. H. C., & R. I. Lewis, 1982. Distribution, composition and general characteristics of the moss banks of the maritime Antarctic. British Antarctic Survey Bulletin **51**, 215—236.

Goddard, D. G., 1979. The Signy Island terrestrial reference sites: XI Population studies on the Acari. British Antarctic Survey Bulletin **48**, 71—92.

— 1980. Biological observations on the free-living mites of Signy Island in the maritime Antarctic. British Antarctic Survey Bulletin **49**, 181—205.

Hale, W. G., 1980. Production and energy flow in two species of *Onychiurus* (Collembola, Insecta Apterygota). Pedobiologia **20**, 274—287.

Lindsay, K. L., 1972. *Nanorchestes antarcticus* Strandtmann; a taxonomic description of the instars. Acarologia **13**, 593—606.

Lister, A., 1984. Studies on the Antarctic predatory mite, *Gamasellus racovitzai*. Unpublished D. Phil. Thesis, University of York.

Luxton, M., 1981. Studies on the prostigmatic mites of a Danish beechwood soil. Pedobiologia **22**, 277—303.
Petersen, H., & M. Luxton, 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos **39**, 287—388.
Strandtmann, R. W., 1967. Terrestrial Prostigmata (Trombidiform mites). Antarctic Research Series **10**, 51—80.
— 1982. Notes on *Nanorchestes* V. Two new species of *Nanorchestes* (Acari: Nanorchestidae) from the Antarctic Peninsula and South Atlantic Islands. Pacific Insects **24**, 252—258.
Tilbrook, P. J., 1967. The terrestrial invertebrate fauna of the maritime Antarctic. Philosophical Transactions of the Royal Society of London, series B **252**, 261—278.
— 1973. The Signy Island terrestrial reference sites: I. An Introduction. British Antarctic Survey Bulletin **33** & **34**, 65—76.
Usher, M. B., & R. G. Booth, 1984. Arthropod communities in a maritime Antarctic moss-turf habitat: three-dimensional distribution of mites and Collembola. J. Anim. Ecol. **53**, 427—441.
— — 1986. Arthropod communities in a maritime Antarctic moss-turf habitat: multiple scales of pattern in the mites and Collembola. J. Anim. Ecol. **55**, 155—170.
West, C., 1982. Life histories of three species of sub-Antarctis Oribatid mite. Pedobiologia **23**, 59—67.

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Synopsis: *Original scientific paper*
Booth, R. G., & M. B. Usher, 1986. Arthropod communities in a maritime Antarctic moss-turf habitat: life history strategies of the prostigmatid mites. Pedobiologia **29**, 209—218.
Fifteen sets of samples were collected from a moss-turf habitat on Signy Island, maritime Antarctica, between December 1980 and March 1982. A total of 27,612 Prostigmata, representing nine species, were extracted from these samples. Three of the taxa, *Ereynetes macquariensis*, *Nanorchestes berryi* and *Eupodes* spp. (mostly *E. parvus*, but also including *E. exiguus* and *E. minutus*) were sufficiently abundant for analysis. It is inferred that the generation time of *Ereynetes* and *Nanorchestes* is two years, and of *Eupodes* is two to three years. A characteristic of Antarctic species is that generation times are in excess of one year, and that the life history strategies are flexible.

Key words: Antarctic, generation time, life history strategy, mites, Prostigmata, soil animals.